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Eocene and Oligocene chitons (Polyplacophora) from the Paris and Hampshire basins

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Abstract. Eocene and Oligocene chitons (Polyplacophora) from the Paris Basin of N France are described along with comparative material from the Hampshire Basin of the UK. The assemblages include eight species, five of which are new: *Ischnochiton fehsei* sp. nov., *Stenoplax monila* sp. nov., *Chaetopleura gaasi* sp. nov., *C. abbessi* sp. nov. and *Tonicella lira* sp. nov. Other taxa in the assemblages are *Leptochiton* cf. *algesirensis*, *I. vectensis* and *S. anglica*.

Introduction

Polyplacophoran molluscs (chitons) have a long but generally sparse fossil record, even from the Cenozoic. Fossil chitons are typically indicators of shallow, inshore shelf facies, similar to the environments they inhabit today. While Eocene-Oligocene shallow marine successions are typically mollusc-rich these shelly faunas include few chitons. Here we report on Eocene-Oligocene chiton assemblages from localities in France housed in the State Museum of Bavaria, together with comparative collections from the UK. Many fossil chiton genera

were established in the nineteenth century, and the relationship between these and modern taxa (Kaas and van Belle 1985a, b, 1987, 1990, 1994, 2006), which are largely described based on soft part characters, can be problematic. Also, fossil taxa have been and can be classified based on head, tail or intermediate valves. The systematic classification follows Sirenko (2006) with minor modification.

In the Eocene the Hampshire (Hampshire–Dieppe) Basin connected across the English Channel to the Paris Basin of northern France (Murray 1992). Mid-late Eocene deposition of shelly faunas (Bracklesham Group, Barton Beds) took place in shallow marine to marginal marine environments. The Eocene Paris Basin also had shallow marine deposition, dominantly of limestones and sands, with later restriction of the Basin represented by evaporites. Tectonism and inversion led to the silting up of the Hampshire Basin in the Oligocene, but the Paris Basin retained a marine connection at least in the early Oligocene.

Material

The following collections were used in this study: State Museum of Bavaria **ZSM** Mol 20060776, Mol 20060779, Mol 20060780, Mol 20060781, Mol 20060782, Mol 20060783, Mol 20060784, Mol 20071427, Mol 20071428, Mol 20071438; Natural History Museum, London specimens **NHM** 66011-3, 62746; Alan Morton **AJM** Colwell Bay CB1-10 and Howgate Bay HB1-6.

Systematic Taxonomy

Class **Polyplacophora** Gray, 1821

Subclass **Neoloricata** Bergenhayn, 1955

Order **Lepidopleurida** Thiele, 1909

Suborder Lepidopleurina Thiele, 1909

Family **Lepidopleuridae** Pilsbry, 1892

Genus ***Leptochiton*** Gray 1847

Leptochiton Gray, 1847a: p. 127. Type species: *Chiton cinereus* Montagu, 1803, by subsequent designation (Gray, 1847b), *non* Linnaeus, 1767 (= *Chiton asellus* Gmelin, 1791).

Leptochiton cf. *algesirensis* (Capellini, 1859)

Fig. 1

1859 *Chiton algesirensis* Capellini: p. 327, pl. 12, Figs 3a-c

1883 *Lepidopleurus maguntiacus* de Rochebrune: p. 58

1893 *Lepidopleurus algesirensis* (Capellini, 1859): Pilsbry: p. 62, pl. 14, figs 20-21

1962 *Lepidopleurus* (L.) *algesirensis* (Capellini, 1859): Malatesta p. 151, fig 7

1978 *Lepidopleurus maguntiacus* Rochebrune, 1882: Janssen: p. 219, pl. 14:11-15, 15:16-17

1985 *Leptochiton* (L.) *algesirensis* (Capellini 1859): Kaas & Van Belle, p. 44, fig.17

1989 *Lepidopleurus* (*Leptochiton*) *algesirensis* (Capellini, 1859): Dell'Angelo & Palazzi, p. 61, pl. 8-13

1999 *Lepidopleurus (Leptochiton) algesirens* (Capellini, 1859): Dell'Angelo & Smriglio, p. 53, pl. 12-13, figs 20-23

2001 *Lepidopleurus (Leptochiton) algesirens* (Capellini, 1859): Dell'Angelo *et al.*, p.145, fig. 2

2004 *Lepidopleurus (Leptochiton) algesirens* (Capellini, 1859): Dell'Angelo *et al.*, p.26, pl. 2, fig. 3

2012 *Lepidopleurus algesirens* (Capellini 1859): Dell'Angelo *et al.* p. 56, pl. 3 fig. D

Material. ZSM Mol 20060780 and 20060781 Gaas, Aquitaine, France; 20060780 A-B two tail valves, one only partial; 20060781F tail valve

Occurrence. Lower Oligocene Rupelian

The tail valves are semi-circular, wider than long (W:L 1.8) with low elevation (H:W 0.23) subcarinate (anterior jugal angle 132°), and with a subcentral rounded mucro (Fig. 1A-D).

The antemucronal area is raised, with a broad, horseshoe shaped jugal fold, ornamented by fine longitudinal to outwardly directed beaded riblets (50-55) of elongate granules (Fig. 1A, D-F). The postmucronal slope is concave, slightly depressed, with radial fine granular ornament (Fig. 1A, D, E). The sutural plates are short, tapering outwards. The ventral surface lacks insertion plates or has an unsplit band, transverse callus grooves radiate outwards beneath mucro (Fig. 1B).

Remarks. The living species was described in detail by Kaas & van Belle, who reported the holotype as unknown or probably lost (1985a, 44-46, fig 17). The genus spans from

Palaeocene-Recent. A combination of longitudinal and radial fine granular ornament, and subcarinate form, are characteristic for *L. algesirensis* tail valves. The Lower Oligocene specimens from Gaas show fewer riblets on the antemucronal area, 50-55, compared with 65-70 in this species reported from the Oligocene of western Germany (= *Lepidopleurus maguntiacus* Rochebrune of Janssen 1978: Dell'Angelo & Palazzi 1989), where collections include a large number of tail plates (126 in Boettger collection; Janssen 1978). A Lower Pliocene tail valve from Spain figured by Dell'Angelo *et al.* (2004, pl. 2 fig 3) is also described as having 65-70 ribs on the antemucronal area. Because of the reduced number of antemucronal riblets the Gaas specimens are considered here as *L. cf. algesirensis*. From the Plio-Pleistocene of Italy, *L. algesirensis* was reported as well as another Recent species *L. bedulli* Dell'Angelo & Palazzi, 1986 that has broadly comparable ornament on the tail plate although the longitudinal rows of tubercles are separated by spaces (Dell'Angelo *et al.* 2013).

Palaeocene-Oligocene leptochitonids are not common, and some uncertainty remains in the generic assignment of Eocene-Oligocene species to *Lepidopleurus* or *Leptochiton* (Dell'Angelo *et al.* 2015). Tail valves of the Palaeocene (mid Danian) species from Denmark, *L. faksensis* Sigwart *et al.*, 2007* have even granular quincunx ornament. (*Note: Although the species description is detailed, multiple holotypes were selected which does not fulfil the requirements of the ICZN (Arts. 16.6, 73) and thus the name should be considered invalid). Articulated fossil specimens and valves from the late Eocene-early Oligocene of Washington State with tail valves having regular fine granular ornament with strong concentric rugae on the post-mucronal area were assigned to the modern species *L. alveolus* Lovén, 1846 (Squires & Goedert 1995). A single intermediate valve from the late

Eocene-early Oligocene of Washington State described as *Leptochiton* sp. has ornament of subgranulose ribs, with differentiated ornament in central and lateral areas (Dell'Angelo *et al.* 2011). Bielokrys (2000) described 4 species of *Lepidopleurus* from the Upper Eocene of the Ukraine: the tail valve of *L. scirpeus* has somewhat similar ornament although differs from *L. cf. algesirensis* in its lenticular form, more anterior mucro and consequent narrow antemucronal area.

Order **Chitonida** Thiele, 1909

Suborder **Chitonina** Thiele, 1909

Superfamily **Chitonoidea** Rafinesque, 1815

Family **Ischnochitonidae** Dall, 1889

Genus ***Ischnochiton*** Gray, 1847a

Type species. *Chiton textilis* Gray, 1828, by subsequent designation (Gray, 1847b:126)

For synonymy see Kaas & van Belle 1990.

Ischnochiton vectensis Wrigley, 1943

(Fig 2)

1943 *Ischnochiton vectensis* Wrigley: 188-9, figs 1-3.

Material. Holotype NHM 66011 intermediate valve, paratypes NHM 66012 head valve, NHM 66013 tail valve. Topotype specimens AJM CB1-10; four intermediate valves, three head valves, three tail valves; AJM HB2, 3, 5, three intermediate valves.

Occurrence. Headon Beds, Colwell Bay (NHM and AJM CB) and Howgate Bay (AJM HB), Isle of Wight. Middle Eocene.

Description. The type material (holotype intermediate valve, NHM 66011; paratypes head valve NHM 66012 and tail valve 66013) of *Ischnochiton vectensis* Wrigley 1943 from the Middle Eocene Headon Beds of Colwell Bay, Isle of Wight was examined for comparison with new collections from the Lower-Middle Eocene of France, as well as new topotype specimens from Colwell Bay, Isle of Wight and additional new material from the contemporaneous succession at Howgate Bay, Isle of Wight collected by Alan Morton (<http://www.dmap.co.uk/fossils/>; Fig. 2). Wrigley's original collection comprised 76 valves, which he assigned to a single species; only the types are in NHM collections. As the type specimens are partly silicified and beekitised, only the type intermediate and head valves are re-figured here (Fig. 2A-C, O-Q). The new, well preserved material from Colwell Bay shows variable morphology of the intermediate valves (10 valves), particularly in the degree of arching of valves and development of radial folds (Fig. 2D-N). Valves are short, wide and rectangular, round-backed and with moderate elevation (Fig. 2C, F, J, N). Wrigley (1943, p.188) noted based on 64 intermediate valves that width was more than three times length, and length was similar to height. The new material of intermediate valves is less broad, (width:length $W:L = 2.5$), moderately elevated (height:width $H:W = 0.4$; elevation terminology following Kaas & van Belle, 1981), and close to as high as long (height:length $H:L = 1.1$). The dorsal surface has one to three narrow elevated jugal folds within a broad central area (Fig. 2A, D, H, L); a low diagonal fold delimits central and lateral areas. The anterior margin is slightly to moderately convex. Broad apophyses (sutural laminae) are thin, smooth, rounded, separated by a wide sinus, insertion plates have a single slit (Fig. 2G,

K). The posterior margin is broadly obtuse to straight, with a slightly protruding apex. The round granular ornament is coarse, tending to coalesce into beaded longitudinal to incurved riblets on the central area (Figs. 1D, H, L; 5B', E'). Granules show single aesthetes (Fig. 2B'-C').

On the ventral surface a narrow triangular ventral apical band extends across the posterior margin, and a transverse thickened callus ridge curves beneath the jugal area across to the lateral margins ('raised centrally in the form of ox horns'; Wrigley 1943, p.188; Fig. 2B, E, I, M). The jugal area is porous (e.g. Fig. 2E).

Wrigley's description of head valves was based on 10 specimens (paratype Fig. 2O-Q), and the new collections include a further three (Fig. 2X-A'). The broad, semicircular head valve, more than twice as wide as long (W:L 2.2), is moderately arched (H:W 0.33), with eight low, narrow radial folds, and fine granular ornament. Insertion teeth (nine) are striated, short, with solid eaves; radial slit rays run between teeth. The posterior margin is nearly straight (173°), crossed by a narrow band-like apical area on the ventral surface.

The tail valve was described by Wrigley (two specimens) as having a distinct sinus in the posterior margin, which is also shown in three new specimens (Fig. 2R-W). The tail valve is short, transversely ovoid and trapezoidal, more than twice as wide as long (W:L 2.2) and low to moderately arched (H:W 0.27). It has a central low mucro and narrow elevated antemucronal area, with granular ornament forming beaded riblets. Apophyses are broad, short, separated by a wide sinus. The postmucronal margin has a shallow invaginated sinus (Fig. 2R, U). The ventral surface has short, unequal, striated insertion teeth (10-11; Wrigley 1943; Fig. 2S, V), solid eaves, porous jugal area.

Remarks. The new well-preserved topotype and contemporaneous material from the Isle of Wight clarifies and allows photographic illustration of the morphology described and illustrated in drawings in the original Wrigley (1943) description. The new material of intermediate valves is variable but overall less wide than originally described, W:L 2.5 rather than 3, and the fairly coarse granular ornament of intersecting quincunx lines tends to coalesce into longitudinal to incurved riblets on the central area. The tail valve has the distinctive posterior sinus noted by Wrigley (1943).

Van Belle (1981) tentatively placed this species in the genus *Lepidochitona* without supporting explanation. Although some shell characters of this species would fit modern genus definitions of *Lepidochitona* (e.g. Kaas & Van Belle 1985b), the overall shape, elevation and central area sculpturing are more *Ischnochiton*-like and thus we follow Dell'Angelo *et al.* (2011) and retain the original combination.

The posterior, or caudal, sinus is an atypical feature of this genus and family. It is however found in species of the Schizochitonidae, Loricidae, Mopaliidae, and Tonicellidae (Sirenko, 2017 pers. comm.). In Sirenko's (2006) revised classification, based on characters of the egg and position of gills, the former two families lie within the Chitonina, the latter two in the Acanthochitonina. Based on this feature of its morphology *I. vectensis* should perhaps be re-assigned in future to a new genus of the Mopaliidae, as an early representative of the family. The general tegmental morphology resembles that of modern *Mopalia*. The more or less central mucro in the tail valve is still similar to the Tonicellidae. Insertion teeth are numerous but much reduced in length centrally, possibly a precursor towards a deeper sinus and slit reduction. However, if this taxon is re-assigned to the

Mopaliidae then early genera like *Heterochiton* and *Allochiton*, which show little similarity to *I. vectensis* are likely a different lineage.

***Ischnochiton fehsei* sp. nov.**

(Fig. 3)

Diagnosis. Intermediate valves broadly rectangular, twice as wide as long, highly elevated, with a pointed posterior apex. Jugal area flanked by low folds and with narrow central fold, indistinct or low diagonal fold delimiting broad central area and narrow lateral areas. Quincunxial, fine to medium, granular ornament.

Derivation of name. Named after Dirk Fehse from Berlin who collected much of the chiton material described in this paper.

Material. ZSM Mol 20060783, Villiers Saint Frédéric, Yvelines, Ile de France; 79 intermediate valves, five head valves, five tail valves. ZSM Mol 20060784, L'Orme, Yvelines, Ile de France; 44 intermediate valves, six head valves, 19 tail valves.

Holotype: ZSM Mol 20060783 C1 intermediate valve (Fig 3A-D); paratypes: head valve ZSM Mol 20060783 A1 (Fig. 3M-P); tail valve ZSM Mol 20060783 B3 (Fig 3U-X)

Occurrence. Lower-Middle Eocene; ZSM Mol 20060783 Lutetian, Level IV; ZSM Mol 20060784 Lutetian Level V.

Description. Intermediate valves (Fig. 3A-L) broadly rectangular, twice as wide as long (W:L 2.2), sub-carinate and highly elevated (H:W 0.52), side slopes straight to gently convex. Anterior margin straight to gently convex, lateral margins rounded, tapering slightly

anteriorly, posterior margin widely v-shaped (c.150°), straight to slightly concave outside pointed apex. Posterior jugal angle close to perpendicular (88°). Quincunxial, fine to coarser granular ornament; granules elongate (Fig. 2 C'). Indistinct low radial folds, three forming jugal area, one pair delimiting narrow lateral areas sometimes with indistinct longitudinal rugae. Sutural laminae sharp, rounded triangular, wide; single insertion slit (Fig. 3C, G, K). Ventral surface with short triangular apical area, very low transverse ridge anterior to radial slit ray across to insertion slit, a second slit ray near posterior margin.

Head valve widely v-shaped to semi-circular (145°), twice as wide as long (W:L 2.2), round-backed with moderate elevation (H:W 0.41), posterior jugal angle slightly obtuse (104°) (Fig. 3M-T). Regular quincunxial ovoid granular ornament (Fig. 3B'), eight low radial ribs. Ventral surface with short triangular ribbon like apical area, 10 grooved insertion teeth separated by slit rays, eaves solid.

Tail valve small, ovoid, wider than long (W:L 1.5), subcentral mucro, highly elevated (H:W 0.47), anterior jugal angle slightly obtuse (98°) (Fig. 3U-A'). Elevated narrow v-shaped jugal area between apophyses and wide, triangular antemucronal area, depressed postmucronal area (Fig. 3W). Large apophyses, rounded, triangular, becoming bilobed rounding into anterior wider insertion teeth, 8-10 insertion teeth projecting slightly, strongly grooved, narrower centrally (Fig. 3U-A'). Regular granular quincunxial ornament. Ventral surface with horseshoe ridge delimiting narrow central jugal area and antemucronal margin.

Remarks. *I. fehsei* sp. nov. is of similar age to slightly older than *I. vectensis* Wrigley 1943 from the Isle of Wight, but differs in having less broad intermediate valves, nearer to twice as wide as long rather than 2-5-3 times (see above and Wrigley 1943), relatively ill-defined shell areas of intermediate valves, higher elevation, and fairly consistent, fine to medium

granular ornamentation by contrast to areas of intersecting riblets formed of coarser, coalesced granules. On the ventral surface transverse thickening is very low and poorly developed compared to *I. vectensis*. The head valve has a more v-shaped posterior margin. The transversely ovoid tail valve lacks the distinct posterior sinus of *I. vectensis*.

Two species of *Ischnochiton* were described from the Upper Eocene of the Dnepr river (Dnepropetrovsk) by Bielokrys (1999). The regular granular ornament of *I. fehsei* differs from the cancellate ornament of *I. cancellatus* Bielokrys, 1999, which has coarse, closely spaced radial ribs on the head (10-17, usually 14-15; 9 specimens), and tail (15-16, 7 specimens) valves. *I. aspersa* Bielokrys, 1999, from the same locality, has fine nodulose ornament, with narrow sinuous ribs on the central area of intermediate and tail valves. This ornament also compares with ornament of longitudinal cords crossed by transverse lamellae on the central area, and radial ribs on lateral areas, in Upper Eocene–Lower Oligocene *I. goederti* Dell'Angelo *et al.*, 2011 from the USA.

Several species of *Ischnochiton* are known from younger Cenozoic rocks, all differing in ornament from *I. fehsei*. Middle Miocene–Recent *I. rissoi* (Peyraudeau, 1826) has concentric and longitudinal fine vermicular ribs, Middle Miocene *I. korytnicensis* Baluk, 1971 has irregular, close-spaced nodules and longitudinal wavy ribs, and Upper Miocene–Pliocene *I. ligustricus* Dell'Angelo *et al.* 2013 has uniform sculpture of irregularly shaped and sized, overlapping granules (Dell'Angelo *et al.* 2015). *I. zbyi* Dell'Angelo & Silva, 2003 from the Pliocene of Portugal has an ornament of longitudinal and radial ribs and sulci.

Genus ***Stenoplax*** (Carpenter MS) Dall, 1879

Type species: *Chiton limaciformis* Sowerby, 1832, by original designation

***Stenoplax anglica* Wrigley, 1943**

(Fig. 4, 5A-H, Y-Z)

1943 *Stenoplax anglica* Wrigley: 189-90, fig. 5

Material. Holotype tail valve NHM 62810 (and for comparison, *S. selseiensis* holotype tail valve NHM 62746), Upper Bracklesham Beds, Isle of Wight. ZSM Mol 20071438, Villiers Saint Frédéric, Yvelines, Ile de France; four head valves (three + fragment) 20071438A-D, five tail valves 20071438E-H, 78 intermediate valves. ZSM Mol 20060784 L'Orme, Yvelines, Ile de France; six tail valves.

Occurrence. Middle Eocene NHM Lutetian (Bartonian), ZSM Mol 20071438 Lutetian, Level IV. ZSM Mol 20060784 Lower-Middle Eocene, Lutetian, Level V.

Description. The holotype of *Stenoplax anglica* Wrigley, 1943 is a tail valve (NHM 62810; Wrigley 1943 fig. 5; Fig. 4A, B) from the Middle Eocene Upper Bracklesham Beds of Selsey, W Sussex, UK; it is a single specimen from this locality. The shield shaped valve is wider than long (W:L 1.24), with a low elevated subcentral mucro, slightly elevated narrow jugal area in the antemucronal area, gently concave postmucronal slope and a depressed postmucronal area. The ornament is fine granulation, and there are concentric growth lines. On the ventral surface, six short, lightly striated insertion teeth are preserved on one half only, and there is a deep narrow jugal tract.

The Lower- Middle Eocene French collections ZSM Mol 20071438 and 20060784 have similarly shield-shaped tail valves, wider than long (W:L 1.56, 1.33 respectively; Fig. 4E-

J). Fine radial granular ornament on the convex antemucronal area appears fairly even, while a concentric ruga creates a broad margin on the concave postmucronal area (Fig. 5Y). Apophyses are short, triangular, thin, rounded, separated by a wide jugal tract. The ventral surface is smooth on the postmucronal area, the jugal tract is depressed, surrounded by a thickened, grooved callus. 11-13 striated thin, lightly striated, short teeth not extending beyond the valve margin. Anterior jugal angle c.110°, elevation low-moderate (H:W 0.26).

Intermediate valves are rectangular, more than twice as wide as long (W:L 2.2), highly elevated and round arched (H:W <0.6), with fine, regular quincunx granular ornament; some granulae show central aesthetes (Fig. 4O-W, 5Z). The regularity of ornament is a feature of the wide rounded central area (Fig. 4M, S, T). The narrow jugal area (50°) is only slightly elevated outside the apical region, the broad central area (109°) is delineated by a slight diagonal ridge against narrow lateral areas; lateral areas show weak longitudinal corrugation that fades into the central area across a low radial ridge. The anterior margin is fairly straight, while the posterior margin is straight to slightly reflexed (173°) and the apex protrudes slightly; the posterior jugal angle is c. 110°. Apophyses are short, thin, rounded, with a broad jugal sinus, insertion plates have a single slit, a single channel layer in eaves. Ventral surface is smooth, with a transverse low triangular callus ridge, the apical area is triangular, very short or forming a narrow ribbon like band across the posterior margin. Two slit rays, one close to posterior margin, the other traversing to a single slit in the insertion plate, lie behind a low thickened transverse ridge within the lateral area.

The head valves (Fig 3K-N) are approaching twice as wide as long (W:L 1.8-2.0), with a widely v-shaped posterior margin (140-145°), moderately arched (H:W 0.31), low radial

ribs (<eight), and fairly coarse, spaced, regular granular ornament, posterior jugal angle (110°). The 9-10 insertion teeth are grooved, thin, , projecting beyond outline, eaves solid. The apical area is very short, triangular, ventral surface is smooth, radial slit rays mark edges of outer insertion teeth slight radial grooves between teeth.

Remarks. *S. anglica* Wrigley, 1943 and *S. selseiensis* Wrigley, 1943 from the Middle Eocene of the Isle of Wight, area both described from single tail valves at the same locality. *S. selseiensis* (Wrigley 1943, fig. 4; Fig. 4C, D) is relatively longer, the same length as width, only gently convex, and has fine granular ornament. The thin, fairly long apophyses are incomplete towards the jugal sinus across a narrow jugal fold. On the postmucronal area concentric growth lines are more pronounced and delineate a marginal rim. On the ventral surface, the jugal area is obscured, short striated insertion teeth (nine; Fig. 4C, Wrigley 1943, fig. 4), do not extend beyond the margin.

***Stenoplax monila* sp. nov.**

(Fig. 5I-X, A'-B')

Diagnosis. Tail valve semi-circular to shield shaped, wider than long, subcentral slightly elevated mucro and triangular jugal area within antemucronal area, apophyses short, wide and rounded. Strong quincunx ornament of fine granules, tending to form longitudinal to incurved riblets on antemucronal area, concentric riblets on postmucronal area. Postmucronal slope straight to depressed, concentric rugae.

Derivation of name. Latin *monile* a string of beads, a reference to the beaded riblets of the ornament

Material. ZSM Mol 20060781 Gaas, Aquitaine, France; 10 tail valves, two head valves, three worn intermediate valves.

Holotype: 20060781 G tail valve (Fig. 5P-S), paratypes 20060781K head valve (Fig. 5I-K), 20060781M intermediate valve (Fig. 5V-X)

Occurrence. Lower Oligocene Rupelian

Description. Tail valves (20060781A-J; Fig 4 P-S, T-U) are semi-circular to shield shaped, widest anteriorly at the gently convex to straight anterior margin, wider than long (W:L 1.7), with elevated, sub-central mucro and moderately elevated triangular jugal fold on convex antemucronal area, low to moderated elevated, rounded anterior profile (H:W 0.35; anterior jugal angle 117°). The postmucronal slope is straight to slightly depressed. The strong quincunx granular ornament is coarser on the antemucronal area, in some valves becomes elongated into riblets, radial to incurved on antemucronal area, concentric on low rugae of the postmucronal area (Fig. 5A'-B'). Apophyses are wide, fairly short, tapering slightly towards lateral margins, separated by broad sinus. The 9-11 insertion teeth are thin, short, lightly striated; eaves solid, not projecting beyond valve margin.

Head valves (20060781 K, L: Fig. 5 I-K, L-O) are semi-circular, twice as wide as long (W:L 2.1), low arched (H:W 0.23), with an obtuse posterior jugal angle $\sim 130^\circ$, posterior margin straight to slightly reflexed (185°). There is regular, fine granular quincunx ornament, concentric growth lines become evident towards the outer margin. The ventral surface has a short, ribbon like apical area, the 12 insertion teeth are short, thin, smooth to lightly striated; eaves solid. Articulamentum shows faint radial rays between insertion teeth.

Intermediate valves, all worn specimens (20060781M-O: Fig. 5 V-X), are short, broadly rectangular, 2.7 times as wide as long and with moderate elevation (0.4), a straight anterior margin, the posterior margin is incomplete but apparently widely v-shaped, lateral margins are rounded. The valve profile is rounded to carinate (posterior jugal angle $\sim 110^\circ$), with an indistinct, slightly elevated jugal fold. Low diagonal ridges separate central and lateral areas. Coarse quincunxial granular ornament coalesces into beaded longitudinal to incurved riblets. Apophyses are rounded, fairly short, extending to lateral margin, single insertion slit; broad shallow jugal sinus. Low transverse thickened v-shaped ridge on ventral surface at junction of central and lateral areas. Slit rays on articulamentum posterior to transverse ridge on lateral areas, and close to posterior margin, apical area short, triangular.

Remarks. *S. monila* differs from Eocene species *S. anglica* and *S. selseiensis* in its coarser granular ornament, coalescing into longitudinal riblets on the antemucronal area of tail valves and the central area of intermediate valves, concentric on the postmucronal area of the tail valve. Like *S. anglica* the tail valve is wider than long, but it has a more distinct v-shaped jugal fold and fairly straight anterior margin, and fewer insertion teeth (9-11 cf. 12). By comparison to the holotype tail plate of the Oligocene *S. veneta* Dell'Angelo & Pallazzi, 1992, *S. monila* has more coarsely granulate ornament, only concentric on the postmucronal area, and the valve is more convex with an elevated mucro, and has fewer insertion teeth. *S. sigillarius* Bielokrys, 1999, from the Eocene of Ukraine has a tail valve as holotype that has strong ornament of spaced, nodulose longitudinal ribs, and the head valve also has strong nodulose radial ribs. *S. quimperensis* Dell'Angelo, Bonfitto & Taviani, 2011 from the upper Eocene–Upper Oligocene of Washington State, USA is a single intermediate valve that has ornament of fine longitudinal striae on the central area and radial striae on

the lateral areas. *S paviai* Dell'Angelo, Giuntelli, Sosso & Zunino, 2014 from the Miocene of Italy has an ornament of undulose grooves on head, intermediate and tail valves.

Family **Chaetopleuridae** Plate, 1899

Genus ***Chaetopleura*** Shuttleworth, 1853

Type species: *Chiton peruvianus* Lamarck, 1819, by subsequent designation (Dall 1879: 296).

For synonymy, see Kaas & Van Belle (1987)

***Chaetopleura gaasi* sp. nov.**

(Fig. 6A-I)

Diagnosis. Tail valve semi-circular, with insertion teeth and large apophyses extending beyond the tegmentum outline. Triangular antemucronal area with elevated narrow jugal fold, strong ornament of longitudinal beaded riblets and nodules, subcentral mucro. Postmucronal area depressed, ornament of fine rugae with scattered nodules. 11 sharp striated insertion teeth. Head valve semi-circular, with an elevated, slightly upturned apical region and widely v-shaped posterior margin, coarse nodular and beaded ornament, 14 rounded radial ribs, 13 sharp insertion teeth projecting beyond tegmentum.

Derivation of name. From the type locality.

Material. ZSM Mol 20060779 Gaas, Aquitaine, France; A-D: 3 tail valves, 1 head valve,

Holotype 20060779A tail valve; paratype 20060779 D head valve

Occurrence. Lower Oligocene Rupelian

Description. The tail valve (Fig. 6A-C, G; 20060779A-C) is semi-circular, wider than long (W:L 1.7), with moderate elevation (H:W 0.31) and slightly oblique anterior jugal angle of 116° . Insertion teeth and large sutural laminae project beyond tegmentum outline. The mucro is subcentral, the triangular convex antemucronal area has an elevated narrow jugal fold, the postmucronal slope is concave and postmucronal area depressed. Anterior margin straight to slightly convex. Strong ornament of longitudinal beaded riblets and nodules on the antemucronal area, concentric fine rugae with scattered nodules on postmucronal area. Apophyses are broad, rounded, lightly grooved outside a narrow jugal sinus crossed by jugal plate, extending across to a fairly square corner beyond the lateral margin (Fig. 6A, G). Ventral surface with horseshoe shaped jugal fold, 11 sharp, striated, insertion teeth, eaves solid (Fig. 6B).

The head valve (Fig. 6D-F, H; 779D) is semi-circular, more than twice as wide as long (W:L 2.3), with an elevated apical region (H:W 0.4 posterior jugal angle 108°), and widely v-shaped posterior margin slightly upturned medially. Coarse nodular and beaded ornament along 14 rounded radial ribs (Fig. 6I). Ventral surface with broad ribbon like apical area that has longitudinal ribs across elevated apex, becoming narrow outwards (Fig. 6E, F). Radial rays across to 13 insertion teeth projecting beyond tegmentum, sharp, grooved (Fig. 6I); eaves solid.

Remarks: *Chaetopleura* currently ranges from the Miocene to Recent. By comparison to *C. angulata* and *C. isabellei* described from the Holocene of Uruguay (Rojas & Urteaga 2011), the ornament on the end valves described here is far stronger and ribs are fewer. On those species the head valves have a less elevated apex, while tail valves have numerous thin,

narrowly spaced ribs on the antemucronal area. The Recent species *C. apiculata* Say, 1830 was reported from the Miocene of Virginia and Maryland (Richards & Harbison 1942). *C. apiculata* tail valves have a pustular scattered ornament on the postmucronal area, where the Lower Oligocene species has mostly ornament of fine rugae with only scattered nodules/pustules. Also, the apophyses on the tail valve of *C. apiculata*, *C. angulata* and *C. isabellei* do not project beyond the lateral margin as in the new species.

***Chaetopleura abbessi* sp. nov.**

(Fig. 6J-N)

Diagnosis. Intermediate valve large, broad, low to moderate elevation, very short apophyses barely projecting beyond the tegmentum. Broad gently rounded central area with narrow elevated jugal fold, coarse ornament of longitudinal beaded ribs outside jugal area; change to radial beaded ribs on very narrow lateral areas.

Derivation of name. From the type locality.

Material: ZSM Mol 20071427, Abbesses, Bourgogne, France; holotype, intermediate valve

Occurrence: Upper Oligocene Chattian

Large, broad and short, rectangular intermediate valve (Fig. 6I-K), well over three times wider than long (W:L 3.6), with a gently rounded profile and low to moderate elevation (H:W 0.3; posterior jugal angle 120°). Apophyses are very short, barely projecting beyond the anterior margin, rounded, well separated across a broad jugal sinus. Narrow triangular, slightly elevated rounded (worn) jugal fold, wide central area, narrow lateral areas

delineated by low diagonal beaded ridge and change of ornament. Anterior margin straight across jugul area, rounding convexly outwards and curving through lateral areas. Posterior margin nearly straight (174°). Coarse ornament of beaded ribs strong outside worn jugal area (Fig. 6N), longitudinal on central area, radial on lateral areas. Ventral surface smooth, short wide ribbon-like apical area across posterior margin, wider and anteriorly triangular in apical region. No insertion plates visible but indications of slit rays.

Remarks. Although this is just a single specimen it is well preserved. The intermediate valve comes from the Upper Oligocene and, although unfortunately no direct comparison is possible since the Lower Oligocene species *C. gaasi* described above comprises only end plates, there are significant morphological differences. The intermediate valve is considerably larger and relatively wider than the head and tail valves from the Lower Oligocene species. The apophyses of the intermediate valve are very short, with a wide jugal sinus, whereas on the tail valve of *C. gaasi* the apophyses are long and wide, projecting well outside the tegmentum, and the jugal sinus is narrow. The very short apophyses differ from the Holocene species *C. angulata*, *C. asperrima* and *C. isabellei* (Rojas & Urteaga 2011), and also the intermediate valve has a considerably higher W:L of 3.6, cf 2.47, 2.75 and 2.4 respectively. *C. asperrima* has coarse beaded longitudinal ribs on the central area more similar to the intermediate valve described here, but lacks the radial ribs on the lateral areas; the other two species have finer ornament. Holocene and Recent *C. asperrima* (Kaas & van Belle 1987) have a variably forward projecting jugal fold on the convex anterior margin which is not seen in the U Oligocene valve. The Holocene species *C. apiculata* Say, 1830 was reported from the Miocene of Virginia and Maryland but not figured (Richards & Harbison 1942).

Suborder **Acanthochitonina** Bergenhayn, 1930

Superfamily **Mopalioidae** Dall, 1889

Family **Tonicellidae** Simroth, 1894

Genus ***Tonicella*** Carpenter, 1873

Type species *Chiton marmoreus* Fabricius 1780:420 (= *Tonicia* Gray, 1847).

For synonymy see Kaas & van Belle (1985b).

Tonicella lira sp. nov.

(Fig. 6O-W)

Diagnosis. Rectangular, thin smooth intermediate valves with low to moderate elevation, anterior margin convex, outward tapering, posterior margin straight, central area broad and gently rounded with straight side slopes, narrow lateral areas slightly elevated with low longitudinal ridges and furrows truncated across slit ray. Head valves semi-circular, posterior margin nearly straight, eight insertion teeth.

Derivation of name. Latin *lira*, reference to the furrowed ornament of lateral areas.

Material: ZSM Mol 20071428, Abbese, Bourgogne, France; two head valves, 10 intermediate valves. Holotype: 20071428 C, intermediate valve; paratype: 20071428 B, head valve

Occurrence. Upper Oligocene Chattian

Description. Intermediate valves (Fig. 6S-X) are rectangular, thin, 2.5 times as wide as long (W:L 2.45), moderately elevated (0.38), subcarinate (posterior jugal angle 109°) posterior margin nearly straight (171°), anterior margin tapering outwards from slightly to moderately convex jugal area, lateral margins fairly straight. The smooth ornament displays very fine microgranulation. The smooth rounded broad central area has a slight narrow jugal elevation and straight side slopes. Indistinct very low ridges or growth lines parallel to anterior margin round at fairly square corners into ridges and furrows of lateral areas. Lateral areas slightly elevated, not greatly distinct from central area, with shallow longitudinal ridges and furrows, depressed above diagonal slit ray (Fig. 6X). Apophyses are triangular, rounded, fairly long and wide, narrow jugal sinus, insertion plate rounded, short with single slit. The ventral surface is smooth, with short ribbon like apical area across entire posterior margin, shallow triangular transverse ridge. Slit ray across to slit on insertion plate, thin transverse slits in narrow, jugal depression. Fine reticulate pitting on articulum exposed on worn surfaces. Eaves thin, spongy.

Head valves (Fig. 5P-R) are semi-circular, twice as long as wide (W:L 2.0), with low to moderate elevation (H:W 0.36), subcarinate (posterior jugal angle 108°), and with the posterior margin nearly straight (172°). Ornament is worn, fine reticulation. The ventral surface is smooth, a short triangular apical area is confined to apical region, radial slit rays cross between insertion teeth. Eight short, lightly grooved insertion teeth, thin spongy eaves.

Remarks. The holotype of *Tonicella tenuissima* (Sandberger, 1859), an intermediate valve from the Early Oligocene (Rupelian) of Germany, was destroyed in the Second World War.

Janssen (1978) described and figured valves from the same location as well as from Upper Oligocene localities in Germany as *T. tenuissima*. He described the intermediate valves as short and strongly vaulted, with a distinct rib separating the broad central area from the narrow lateral areas of intermediate valves, and having the posterior margin tapering to a pointed apex. Head valves were described as having nine insertion slits between long, unequal, thickened insertion teeth.

From the Eocene of the Ukraine *T. implumis* Bielokrys, 1999 intermediate valves (~150 valves, ~80 well preserved; type is a tail valve) have a pointed apex, lack the ridging on lateral areas and squarish lateral margins, and on the ventral side have a more defined transverse ridge. The head valve has weak radial furrows and insertion teeth extending beyond the anterior margin.

Several new species figured but not described from the Lower–Middle Eocene (Ypresian–Lutetian) of France as Le Renard (mss 1997, <http://www.somali.asso.fr/fossils/biotaxis.php>) include two species with smooth to microgranular ornament, *T. inornata* and *T. bimucronata*. Intermediate valves of both these taxa are less broad (W:L <1.5–2.5 and >1.7, respectively), and the former has a prominent transverse ventral ridge. Other Le Renard mss. 1997 species (*T. undulans*, *T. simplex*, *T. raincourti*, *T. semivittata*) from the Eocene have well defined ornament on valves.

T. sp. cf. T. venusta Clark, 1999 from the Pliocene of southern California, USA was compared with the modern species on the basis of remnant colour patterns (Vendrasco *et al.* 2012). By comparison with the Oligocene material described here, the intermediate valves are flatter, have a w-shape to the posterior margin, broad jugal sinus, and strong

transverse ridge on the ventral surface. Vendrasco *et al.* (2012) also reported fossils of the genus from the Miocene of Japan and Pleistocene of the USA.

The smooth ornament and spongy eaves are characteristic features of *Tonicella*, although these are also found in some species of *Lepidochitona* Gray, 1821, from the same family. *Tonicella* originated in the north Pacific (Sirenko 1974), and a palaeogeographical argument would throw doubt the occurrence of the genus in Europe before the Pliocene (Sirenko, pers. comm. 2017).

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Figure Captions

Figure 1. *Leptochiton cf. algesirens*, Gaas, Aquitaine, France. ZSM Mol 20060780; A-E 20060780 A, tail valve, dorsal, ventral, anterior, left lateral views, detail of granular, beaded riblet and fine granular radial ornament on antemucronal and postmucronal areas respectively. F ZSM Mol 20060780 B, tail valve, detail of beaded riblet ornament on antemucronal area. Scale bars A-D 1 mm, E-F 200 μ m.

Figure 2. *Ischnochiton vectensis*, Colwell Bay, Isle of Wight. A-C NHM 66011, holotype, intermediate valve, dorsal, ventral and posterior views; D-G CB 2, intermediate valve, dorsal, ventral, posterior and left lateral views; H-K CB 4, intermediate valve, dorsal, ventral, posterior and right lateral views; L-N, CB 3, intermediate valve, dorsal, ventral and posterior views; O-Q NHM 66012, head valve, dorsal, ventral and posterior views; R-T, CB 8, tail valve, dorsal, ventral and anterior views; U-W, CB 9, tail valve, dorsal, ventral and anterior views; X-Z CB 6, head valve, dorsal, ventral, posterior views; A' CB5, head valve, right lateral view; B'-C', CB 6 and 4, detail of ornament. Scale bars A-Q 1 mm, R-A' 0.5 mm, B'-C' 0.1 mm.

Figure 3. *Ischnochiton fehsei* n. sp. Villiers St Frédéric, Ile de France, Yvelines, France. A-D, ZSM Mol 20060783 C1, intermediate valve, holotype, dorsal, ventral, right lateral and posterior views; E-H, 20060783 I1, intermediate valve, dorsal, ventral, right lateral and posterior views; I-L, 20060783 D7, intermediate valve, dorsal ventral, right lateral and anterior views; M-P, 20060783 A1, head valve, paratype, dorsal, ventral, right lateral and posterior views; Q-T, 20060783 A3, head valve, dorsal, ventral, left lateral and posterior views; U-X, 20060783 B3, tail valve, paratype, dorsal, ventral, right lateral and top dorsal views; Y-A', 20060783 B4, trail valve, dorsal, ventral and anterior views; B' 20060783 A1, head valve, detail of ornament and insertion teeth. Scale bars A-A' 1 mm, B' 0.5 mm.

Figure 4. A-B, *Stenoplax anglica*, NHM 62810, tail valve , holotype, Colwell Bay, Isle of Wight, dorsal and ventral views; C-D *Stenoplax selseiensis*, tail valve, holotype, Colwell Bay, Isle of Wight, dorsal and ventral views; D-T *Stenoplax anglica*, ZSM Mol 20071438 Franche-Comte, Haute Saone, France; E-F 20071438 D, tail valve, dorsal and ventral, views; G-J, 20071438 G tail valve, dorsal, ventral, right lateral and anterior views; K-N, 1438 B, head valve, dorsal, ventral, posterior and right lateral views; O-R, 20071438 I intermediate valve, dorsal, ventral, posterior and right lateral views; S-U, 20071438 M, intermediate valve, dorsal, ventral and posterior views; V-W, 20071438 J, intermediate valve, dorsal and right lateral views. Scale bars A-N 0.5 mm, O-W 1 mm.

Figure 5. A-H, *Stenoplax anglica*, 20060784 Ile de France, Yvelines; L'Orme, France; A-D, 20060784 A, head valve, dorsal, ventral, posterior and left lateral views ; E-H, 20060784 C, tail valve, dorsal, ventral, anterior and left lateral views. I-U, *Stenoplax monila* n. sp. ZSM Mol 20060781 Gaas, Aquitaine, France; I-K, head valve, paratype, dorsal, ventral and posterior views; L-O, 20060781 L, head valve, dorsal, ventral, right lateral and posterior views; P-S 20060781 G, tail valve, holotype, left lateral, dorsal, ventral and anterior views; T-U, 20060781 B, tail valve, dorsal and right lateral views; 20070781, V-X, 20060782, M, intermediate valve, paratype, dorsal, ventral and posterior views. Y-B' details of *Stenoplax* ornament; Y-Z *S. anglica*, Y, 20060784 Ile de France, Yvelines; L'Orme, France, 20060784 C, tail valve, right lateral corner showing change from radial antemucronal granular ornament to concentric postmucronal; Z, ZSM Mol 20071438 Franche-Comte, Haute Saone, France, 20071438 U, intermediate valve showing regular granules with some central aesthetes; A'-B' *Stenoplax monila* n. sp. ZSM Mol 20060781 Gaas, Aquitaine, France; A', 20060781 B. tail valve showing change from elongate granules in longitudinal to incurved riblets on the

antemucronal field to round granules and concentric bands on the postmucronal area; Scale bars A-H, P-X 1 mm, I-O 0.5 mm, Y-B' 200 μ m.

Figure 6. A-I, *Chaetopleura gaasi*, n. sp. ZSM 20060779 Gaas, Aquitaine, France; A-C, G, 20060779 A, tail valve, holotype, dorsal, ventral, anterior and right lateral views; D-F, H-I, head valve, paratype, dorsal, ventral, posterior and right lateral views, detail of beaded ornament on ribs and insertion teeth. I, J-N, *Chaetopleura abbessi* n. sp. ZSM Mol 20071427, Abbesses, Bourgogne, France; J-M, intermediate valve, holotype, dorsal, ventral, posterior and left lateral views, detail of beaded ornament of central area. O-W, *Tonicella lira* n. sp. 20071428 Abbesses, Bourgogne, France; O-Q, 20071428 B, head valve, dorsal, ventral and posterior views; R-U, 20071428 C, intermediate valve, dorsal, ventral, anterior and right lateral views; V, 20071428 D, intermediate valve, dorsal view; W, 20071428 I, detail of very fine perforate ornament, slightly elevated lateral areas with low ridges and furrows Scale bars A-H, J-V 1 mm; I, N 0.5 mm.

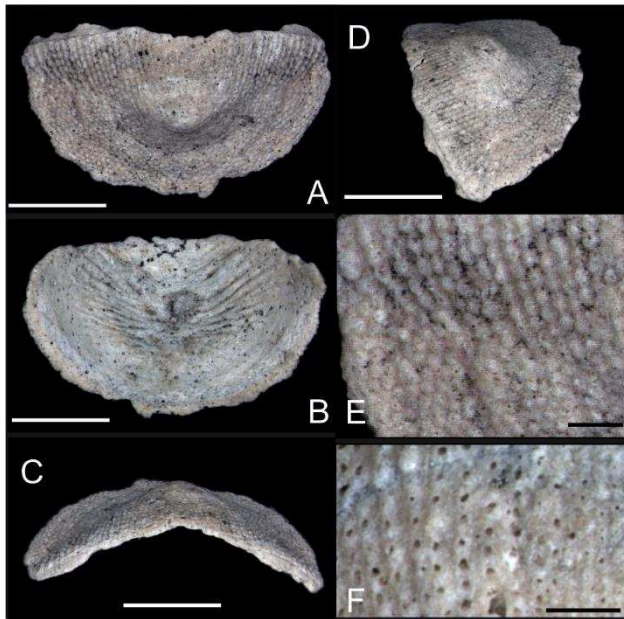


Fig 1

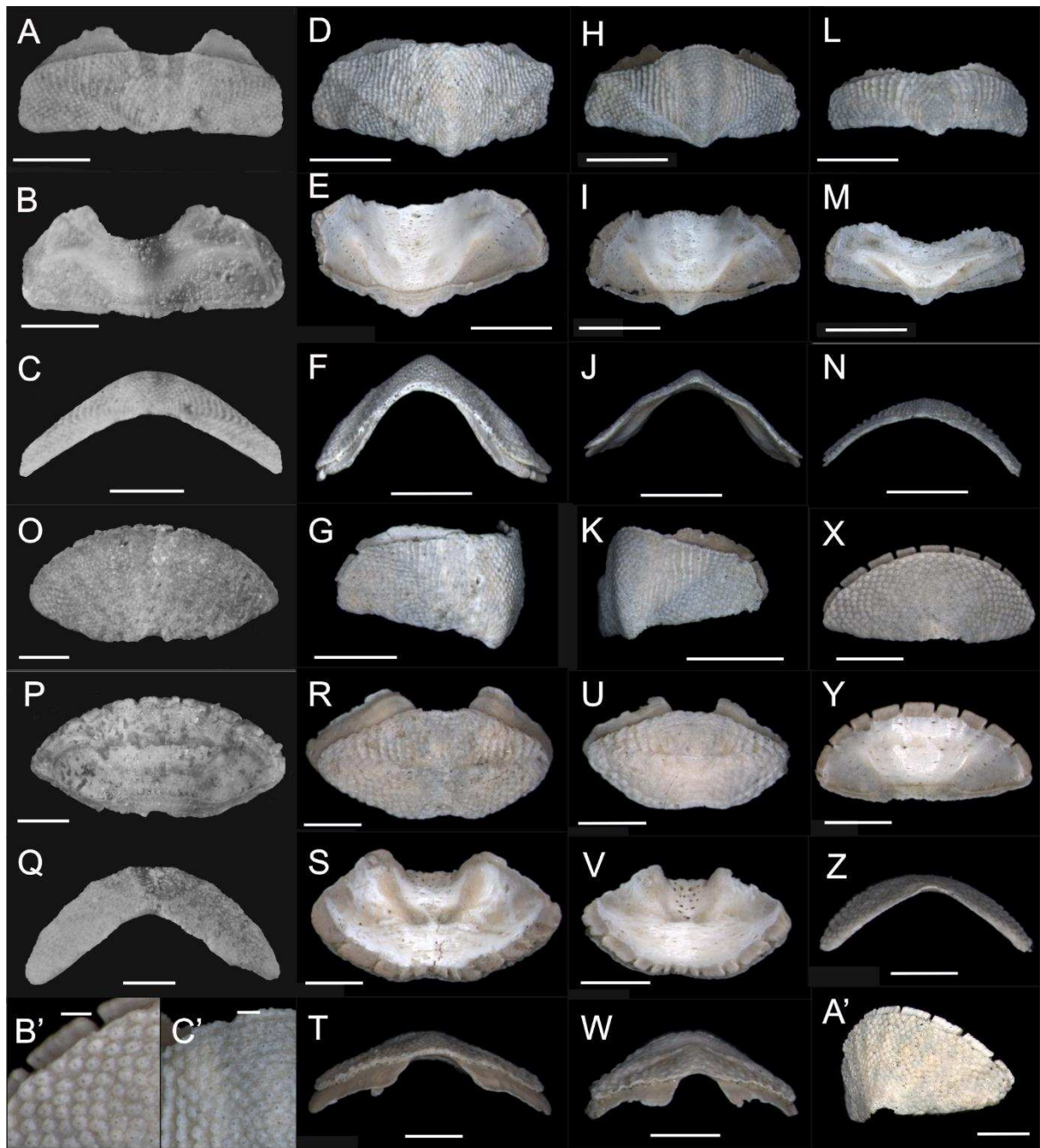


Fig 2

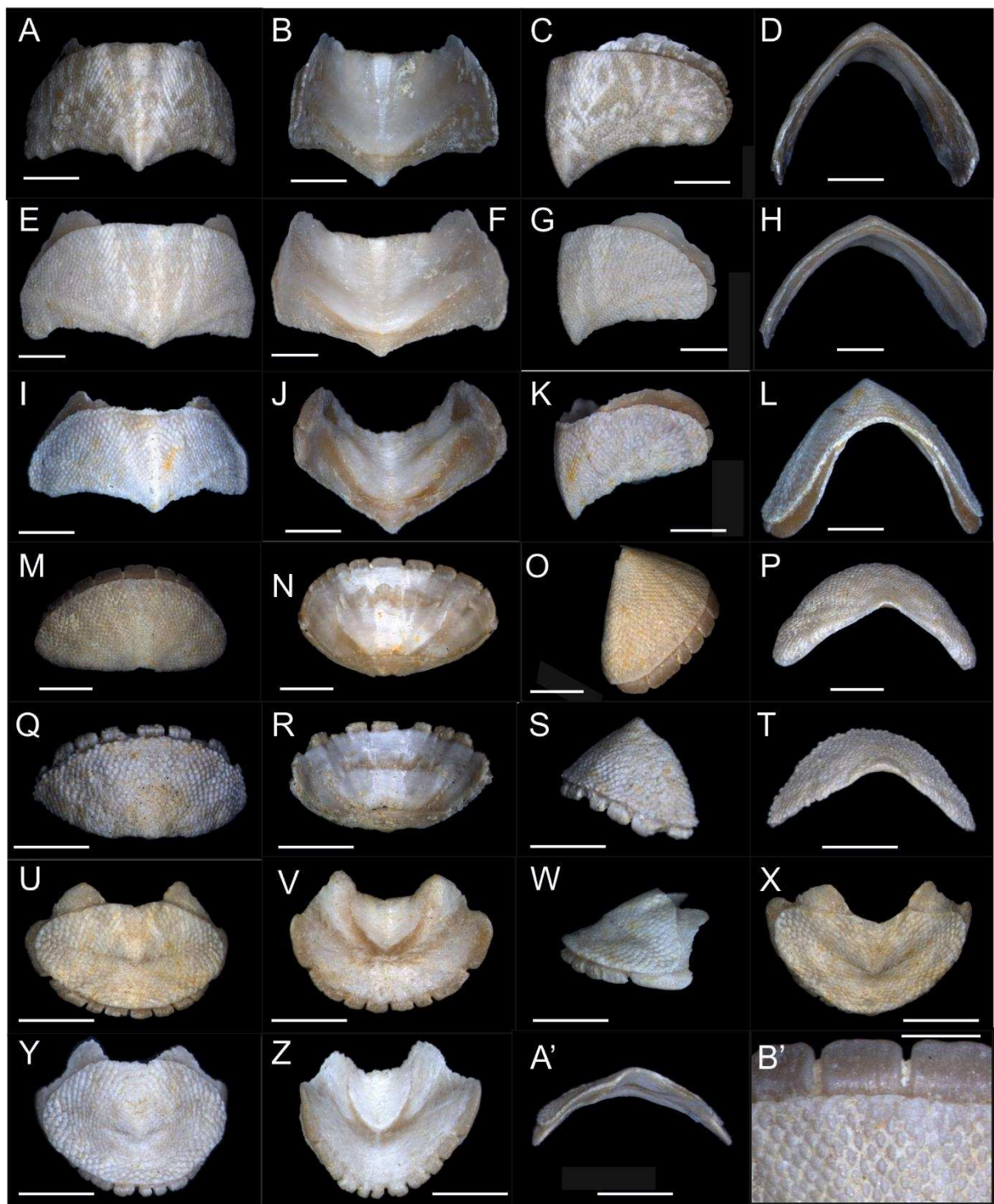


Fig 3

Fig 4

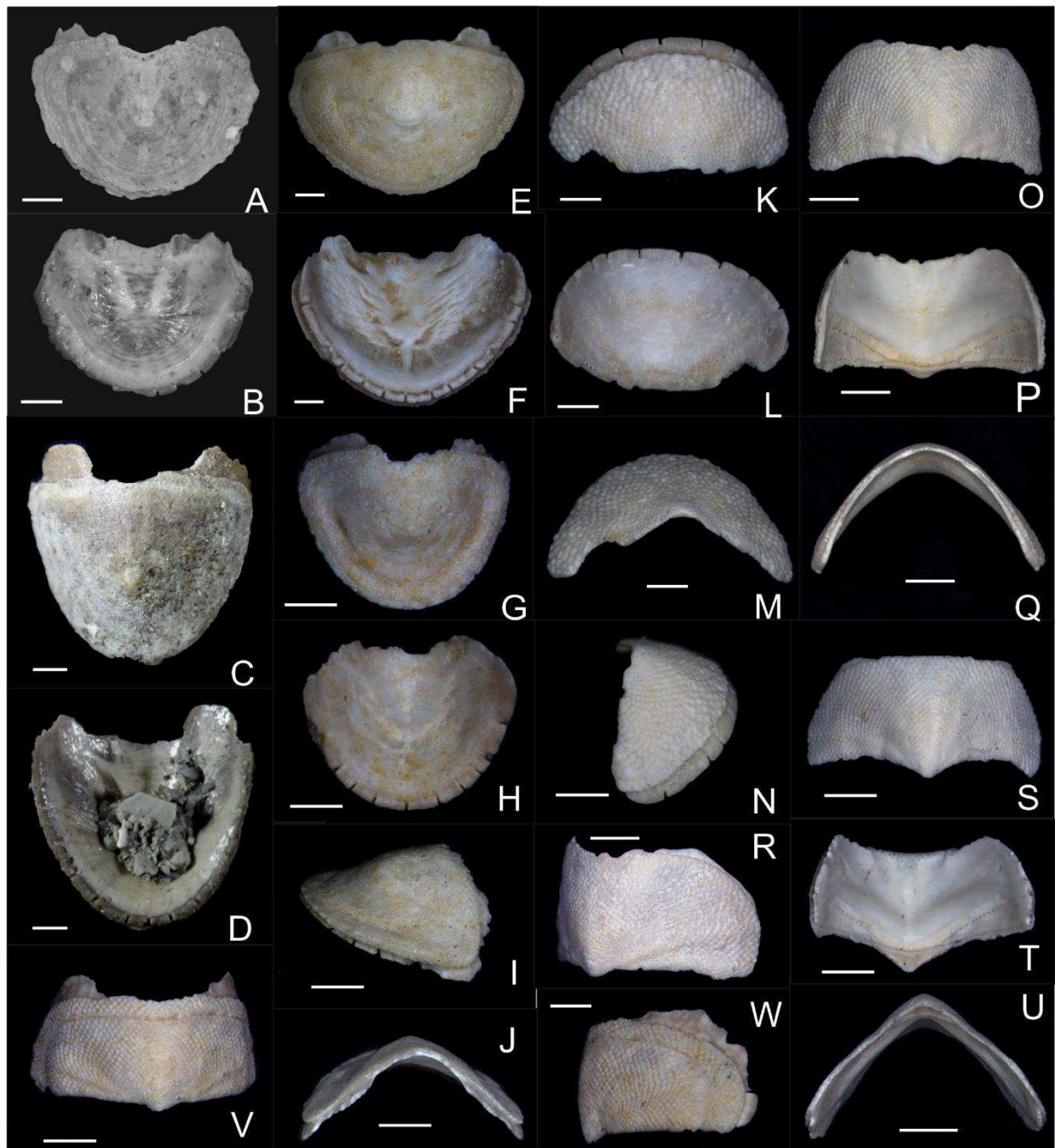


Fig 5

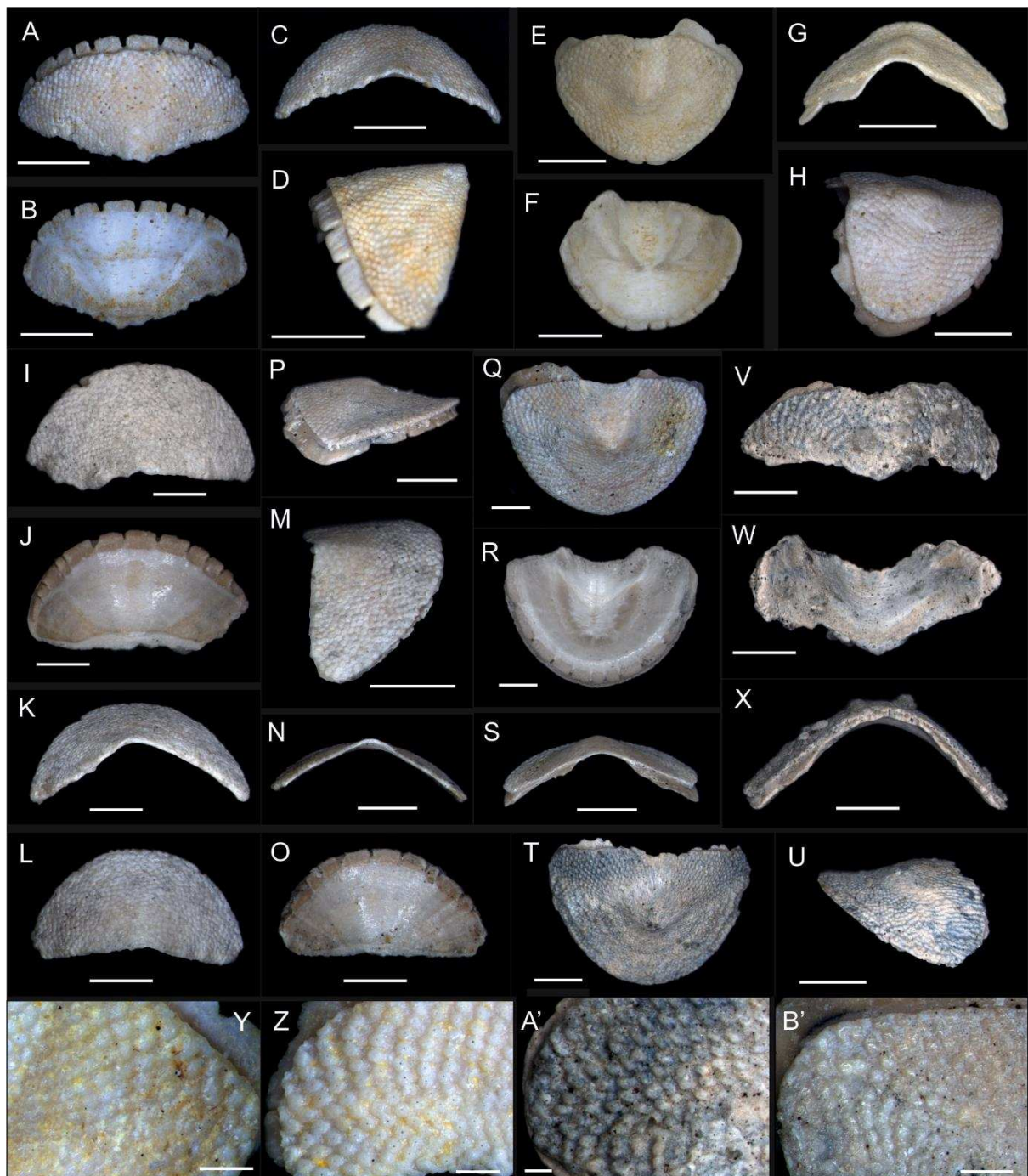


Fig 6

